



Effects of developmental acclimation on fitness costs differ between two aphid species

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ABSTRACT

Most ectotherms are able to increase their tolerance to heat stress via the acclimation response. However, there is ongoing debate about whether the acclimation response is associated with fitness costs, and what factors can affect the consequences of acclimation are still unclear. To elucidate this, we sought to determine whether fitness costs varied with acclimation conditions in two cereal aphids, *Sitobion avenae* and *Rhopalosiphum padi*. Thus, the basal and inducible thermal tolerances (maximum critical temperature [CT_{max}]) and fitness traits (proportion of adult emergence, adult longevity, fecundity, and population parameters) of adult aphids were measured under three conditions of developmental acclimation: 1) 22 °C constant temperature (no acclimation), 2) 22 °C + 34 °C for 2 h per day (low daytime temperature), and 3) 22 °C + 38 °C for 2 h per day (high daytime temperature). We found that the thermal tolerances of both species were significantly higher following developmental acclimations, where higher basal and inducible thermal tolerances were observed in *R. padi* than in *S. avenae*. Low daytime temperature acclimation conditions (34 °C) resulted in negligible reproductive costs and improved the intrinsic rates of population increase in both species. In contrast, substantial fitness costs were detected in both species in response to high daytime temperature acclimation (38 °C), especially for *S. avenae*. Our results indicate that the effects of acclimation conditions on fitness costs differ between the two aphid species. These findings will not only enhance our understanding of species dynamics in the context of climate change but could also potentially improve pest control efforts.

1. Introduction

Global climate change has not only led to continually increasing in average atmospheric temperatures (Lin and Franzke, 2015), but has also increased the frequency and intensity of extreme heat events (Easterling et al., 2000; IPCC, 2013). Climate change has already brought about several ecological consequences, such as changes in population dynamics (Welbergen et al., 2008), community composition (Lomeli-Flores et al., 2010), and the diversity and thermal boundaries of species (Deutsch et al., 2008; Kellermann et al., 2012). In comparison to moderate increases in mean temperatures, frequent high-temperature events that have been directly linked to survival in species may be particularly challenging for organisms to cope with (Fischer et al., 2014), and are considered to be important agents of selection (Hoffmann et al., 2003).

Organisms can increase their thermal tolerance by evolutionary and plastic responses (Chevin et al., 2010; Overgaard et al., 2011; MacLean

et al., 2017), which both play an important role in coping with variations in environmental conditions (Fischer and Karl, 2010; Esperk et al., 2016; Kingsolver and Buckley, 2017). Plastic responses to fluctuations in environmental conditions have been reported in a multitude of species, including arthropods (Lachenicht et al., 2010; Chidawanyika and Terblanche, 2011; King et al., 2014, 2015), mollusks (Littlewood, 1989; Scheil et al., 2011), reptiles (Kosh and Hutchison, 1972; Guderley and Seebacher, 2011), birds (McKechnie et al., 2007; Hepp and Kennamer, 2012), and even mammals (Hansen and Boonstra, 2000; Nespolo et al., 2001). Two main forms of plastic responses to thermal stress—hardening and acclimation—have been frequently discussed in previous studies (Fischer et al., 2010; Fischer and Karl, 2010). Hardening is defined as a mechanism by which thermal tolerance is increased under extreme temperatures following a brief pre-exposure (typically for a few hours) to a sub-lethal temperature (Bowler, 2005), whereas acclimation may involve longer periods of pre-exposure, typically for a few days or even weeks (Esperk et al., 2016).

Abbreviations: NA, No acclimation; LA, Low daytime temperature acclimation; HA, High daytime temperature acclimation

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Despite the benefits of heat acclimation on thermal tolerance, heat acclimation is often accompanied by deleterious fitness costs (Hoffmann, 1995; MacLean et al., 2017). These costs, which have been most thoroughly explored in insects, include delayed development (Vladimír and Michaela, 2009; Wang et al., 2015), decreased larval viability and fecundity in *Drosophila* (Loeschcke et al., 1994; Krebs and Feder, 1998), and reduced rates of parasitism in the pest *Trichogramma carverae* (Scott et al., 1997). However, in some studies, acclimation has been reported to occur with low costs (Huey et al., 1995; Minois, 2000), or without any fitness costs at all (Hoffmann and Hewa-Kapuge, 2010). It has been well established that benefits of acclimation vary across exposed conditions (Allen et al., 2012; Alemu et al., 2017) and species (Hazell et al., 2010; Overgaard et al., 2011). And this raises the question of whether fitness costs also associate with the two factors?

Here, we tested whether the fitness costs of plastic responses may vary with acclimation conditions in two cereal aphids—*Sitobion avenae* and *Rhopalosiphum padi*—both of which are important global pests, usually coexist in many cereal-growing regions (Vickerman and Wratten, 1979; Lu et al., 2016), and differ in their temperature preferences. These two species occupy different temporal niches, where *S. avenae* appears earlier in the cereal-growing season, and *R. padi* becomes dominant at the season's end (Asin and Pons, 2001). *Sitobion avenae* is relatively dominant in most temperate regions (e.g., Spokane [47°39' N; Clement et al., 2004], Göttingen [51°32' N; Thies et al., 2005], and Prague [50°05' N; Leslie et al., 2009]), whereas *R. padi* is relatively dominant in higher-temperature regions (e.g. as Yibin [28°46' N; Huang et al., 1996], Santa Maria [29°41' S; Parizoto et al., 2013], and Luxor [25°41' N; SIman, 2006]).

In the present study we addressed the following questions: (1) Does thermal tolerance and acclimation capacity vary with acclimation conditions between the two aphid species? (2) If so, do the fitness costs of plastic responses to temperature exposure vary with acclimation conditions? In order to assess plastic responses in the two aphid species, we investigated adult basal and inducible tolerances by observing CT_{max} (maximum critical temperature [CT_{max}]) and examining fitness traits (proportion of adult emergence, longevity, fecundity, and population parameters) after exposure to three developmental acclimation conditions (22 °C constant temperature, 22 °C + 34 °C for 2 h per day, and 22 °C + 38 °C for 2 h per day).

2. Material and methods

2.1. Insects and rearing

S. avenae and *R. padi* were collected from a wheat field near Linfen, China (35°55'N, 111°16'E) in May of 2016. The two species were sent to the laboratory, where one clone per species was established via parthenogenesis. All aphids were maintained in rearing rooms for more than one year prior to the beginning of experiments, which were performed on 10–20 cm tall wheat seedlings. Pots with seedlings were placed in screened cages (60 × 60 × 60 cm) in controlled rearing rooms (22 ± 0.5 °C, 50–60% relative humidity, with a 16:8 h L:D photoperiod). New seedlings were provided every week.

2.2. Conditions of developmental acclimation

Three climate chambers (RXZ-280B; Jiangnan Ltd., Ningbo, China) were used to program three developmental acclimation conditions during the nymphal period: (1) 22 °C constant temperature (no acclimation: NA), (2) 22 °C + 34 °C for 2 h per day (low daytime temperature acclimation: LA), and (3) 22 °C + 38 °C for 2 h per day (high daytime temperature acclimation: HA) (Fig. 1).

In the NA treatment, the temperature was kept constant at 22 °C throughout the experiment. In the temperature-ramping phase of the LA and HA treatments, temperature was increased linearly from 8:00 h to reach a maximum (34 or 38 °C) at 12:00 h, maintained for 2 h, and

subsequently decreased to 22 °C by 16:00 h. For the remainder of the day, temperature was kept constant at 22 °C. The relative humidity in each chamber was set at approximately 50%. The photoperiod was set to 16 h L: 8 h D, where the light period was from 06:00 to 22:00 h. The temperature in each chamber was recorded at 20 min intervals using data loggers (U23-001; Onset Ltd. Bourne, USA). Differences in the average daily temperatures were small among the three developmental acclimation conditions (22, 24.25, and 25 °C, respectively), where the averages were lower than the optimum temperatures for both species (28.5 °C for *R. padi* and 26.5 °C for *S. avenae*) (Asin and Pons, 2001). Changes in survival and reproductive traits for the two aphids have been shown to be minimal in this temperature range (Asin and Pons, 2001).

2.3. Experimental manipulation

2.3.1. Experiment 1: Effects of developmental acclimation on the CT_{max} of adults

Preliminary experiments were performed in both species to determine the length of time necessary for newly born aphids (< 6 h old) to develop into adults following exposure to the three conditions of developmental acclimation. For all treatments, newly emerged nymphs that had developed into adults were observed beginning on the 7th day, and all nymphs in all treatments had developed into adults by the 9th day.

To test basal and inducible thermal tolerances after exposure to different acclimation conditions, the two species were treated separately to eliminate any possible interspecific competition. For both species, one group of 100 newborn aphids (< 6 h old) was placed in each of the three acclimation chambers at 7:00 h. Aphids in each acclimation chamber were reared on wheat seedlings (height 2–3 cm) in a rearing pot (approximately 50 seedlings per pot) placed inside a screen cage. The seedlings were watered every 2–3 days to maintain freshness. To prevent the aphids from escaping, host plants were not replaced during the experiment.

On the ninth day of the acclimation treatment, 30 adults per acclimation condition were randomly selected, and their CT_{max} was tested as described by Zhao et al. (2017). Briefly, the aphids were placed individually in the holes (diameter 5 mm, depth 5 mm) of a honey comb plate (80 × 80 mm) attached to nylon gauze (200 mesh size) on one side and a transparent plastic board on the other side. The honeycomb plate was placed vertically within a double-glazed container (diameter 100 mm, height 100 mm) heated by a glycol bath (Ministat 230-cc-NR; Huber Ltd., Germany; accuracy ± 0.01 °C). Temperatures in the container were monitored using a thermocouple (Pt100) connected to the bath equipment. After 5 min of equilibration at 22 °C, the temperature was increased at a rate of 0.5 °C min⁻¹ from 22 to 30 °C and then from 30 to 45 °C at 0.1 °C min⁻¹. Aphids were observed for movement using a SONY® video camera (HDR-PJ50E; Sony Corporation, Shanghai, China). The CT_{max} was defined as the temperature at which each aphid last moved its legs or antenna.

2.3.2. Experiment 2: Effects of developmental acclimation on fitness traits

To assess how conditions of developmental acclimation affected fitness traits, 48 newborn nymphs (< 6 h old) from each species were held individually in rearing units until adulthood under the respective acclimation regimes, and subsequently moved to 22 °C (constant temperature conditions) as follows. Rearing units were constructed from hollow plastic tubes (15 mm diameter, 70 mm length), which were sealed by a sponge plug (17 mm diameter, 20 mm length) on the upper end. A single aphid was placed on a newly excised wheat leaf (50 mm length) that was held firmly by a 10 mm slit in another sponge plug (17 mm diameter, 20 mm length) at the bottom of the rearing unit. Twenty-four rearing units were placed separately in the 24 holes (17 mm diameter) of a multiporous lucite plate (200 mm length, 135 mm width) held in a tray containing water deep enough to wet the

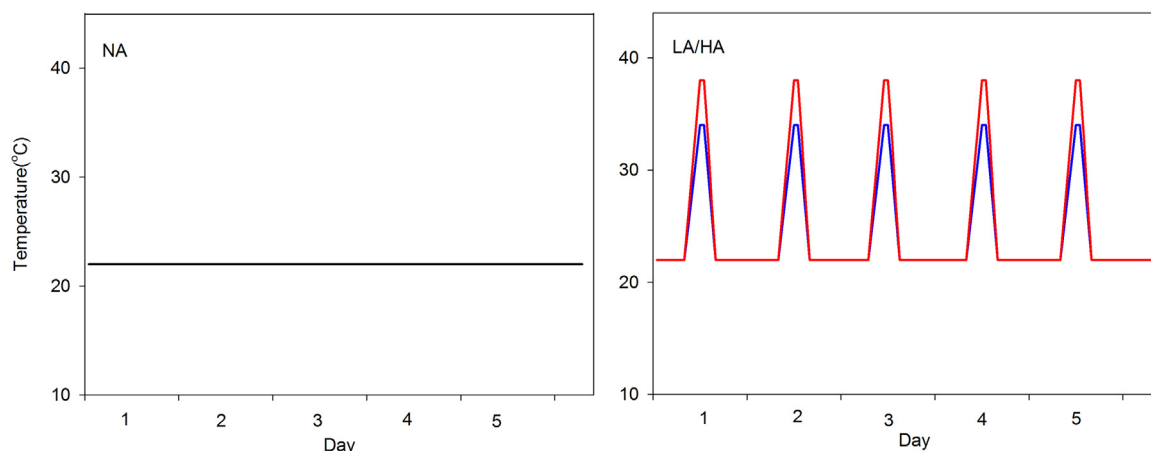


Fig. 1. Diagram of acclimation conditions during the experiments. NA (no acclimation), LA (low daytime temperature acclimation), and HA (high daytime temperature acclimation) represent a constant temperature of 22 °C (black line), 22 °C + 34 °C for 2 h per day (blue line), and 22 °C + 38 °C for 2 h per day (red line), respectively (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

bottom sponge plug. Two trays (48 rearing units in all) were placed in each acclimation chamber. Aphids were transferred to new rearing units every 2–3 days. Nymphal development and survival were inspected at 08:00 h each day, and the tubes with dead aphids were removed. Once nymphs reached adulthood, adults were moved to a constant temperature (22 °C) to promote uniform growth under similar environmental conditions. The reproduction and survival of the adults in each tube were checked once a day at 08:00 h. Newborn nymphs and dead adults were removed without disturbing the experimental aphids.

The following traits were determined for all aphids: the proportion of adult emergence, longevity, and fecundity. The proportion of adult emergence was calculated as the percentage of nymphs still alive at adulthood. Adult longevity was calculated as the period from adult emergence until death. Fecundity was the total number of offspring per adult. To test the effects of developmental acclimation conditions on population parameters, the finite rate of increase (λ), the intrinsic rate of population increase (r_m), net reproductive rate (R_0), and mean generation time (T) were calculated for each treatment using Pop Tools 3.2.5 (Hood, 2011).

2.4. Statistical analyses

All statistical analyses were performed using SPSS version 20 (SPSS Inc.; Chicago, IL, USA). The data for the traits studied met the basic assumptions of normality based on Shapiro-Wilks test and were therefore analyzed using parametric tests. The effects of species and developmental acclimation conditions on CT_{max} , fecundity, and longevity were examined via a two-way ANOVA using the GLM procedure. Because of significant interactions of species and developmental acclimation conditions on main traits, independent sample t -tests and one-way ANOVAs were used to further analyze the effects of species and acclimation treatments at each level of the other factor. Posthoc comparisons involved Tukey or Games-Howell tests depending on whether treatment variances were equal or unequal. The effects of species and acclimation conditions on the proportion of adult emergence were estimated using a Chi-square analysis of a 2×3 contingency table, and differences between acclimation conditions or between species were determined via a separate contingency table with Bonferroni adjustment.

3. Results

3.1. Thermotolerance responses (CT_{max}) following developmental acclimation

There were significant effects of species, developmental acclimation condition, and their interaction on CT_{max} (Table 1). In addition, we observed that the conditions of developmental acclimation exerted significant effects on CT_{max} in both aphid species (*S. avenae*: $F_{2,84} = 24.737$, $P < 0.001$; and *R. padi*: $F_{2,87} = 35.989$, $P < 0.001$), where CT_{max} values tended to increase with the daily maximum temperature (Fig. 2). In *S. avenae*, the CT_{max} of aphids maintained at the constant temperature of 22 °C (NA; 38.54 ± 0.99 °C) increased by 1.17 ± 0.21 °C and 1.25 ± 0.20 °C following low (LA) and high (HA) acclimation conditions, respectively. In *R. padi*, CT_{max} increased by 0.56 ± 0.14 °C and 1.32 ± 0.14 °C following LA and HA, respectively, in comparison to the NA treatment (39.05 ± 0.36 °C). Additionally, *R. padi* exhibited a higher thermal tolerance than *S. avenae* in all acclimation treatments (NA: $t = -2.499$, $df = 32.701$, $P = 0.018$; HA: $t = -4.043$, $df = 48.339$, $P < 0.001$), except in the case of LA ($t = 0.722$, $df = 61$, $P = 0.473$).

Table 1

Effects of developmental acclimation condition, species, and their interactions on CT_{max} (°C), fecundity (nymphs/adults), and longevity (days) as determined via two-way ANOVA. The “*” and “***” symbols represent significant differences at the $P < 0.05$ and $P < 0.01$ levels, respectively.

Factor	Df	MS	F	P
<i>CT_{max}</i>				
Species	1	4.718	11.719	0.001**
Acclimation conditions	2	24.140	59.964	< 0.001**
Species × acclimation conditions	2	2.174	5.400	0.005**
Error	171	0.403		
<i>Fecundity</i>				
Species	1	33,833.146	139.866	< 0.001**
Acclimation conditions	2	14,735.053	60.915	< 0.001**
Species × acclimation conditions	2	682.740	2.822	0.062
Error	220	241.897		
<i>Longevity</i>				
Species	1	639.750	16.628	< 0.001**
Acclimation conditions	2	2038.890	52.995	< 0.001**
Species × acclimation conditions	2	322.976	8.395	< 0.001**
Error	224	38.473		

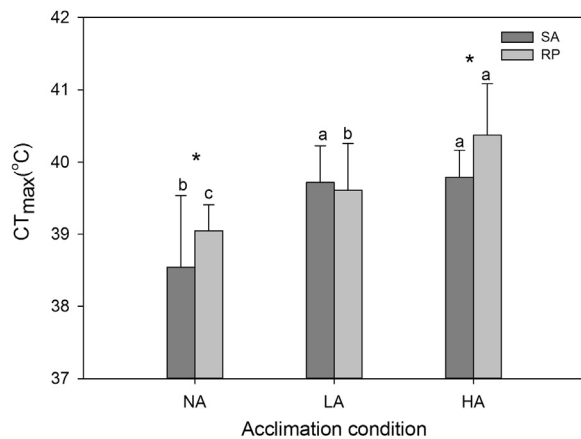


Fig. 3. Effects of developmental acclimation condition on CT_{max} (mean $\pm$ SD) in the two aphid species. Different letters above the bars indicate significant differences between acclimation conditions for each species (one-way ANOVA, $P < 0.05$). “*” represents significant differences between the two species within each acclimation condition (t -test, $P < 0.05$). SA = *Sitobion avenae*, RP = *Rhopalosiphum padi*.

3.2. Proportion of adult emergence following developmental acclimation

The conditions of developmental acclimation were observed to exert significant effects on the proportion of adult emergence in both *S. avenae* ($\chi^2 = 49.192$, $df = 2$, $P < 0.001$) and *R. padi* ($\chi^2 = 25.299$, $df = 2$, $P < 0.001$). Similar to the proportion of adult emergence observed in the NA treatment, nearly all newly born aphids were found to attain adulthood after exposure to LA; however, a significant decline was observed in both *S. avenae* (37.5%) and *R. padi* (66.7%) in response to HA (Fig. 3). In addition, the proportion of adult emergence in *R. padi* was higher than that of *S. avenae* under all acclimation regimes, and was significantly higher in response to HA ($\chi^2 = 9.412$, $df = 1$, $P = 0.002$) (Fig. 3).

3.3. Effects of developmental acclimation on adult performance

3.3.1. Effects of developmental acclimation on adult fecundity

There were significant effects of species and developmental acclimation on adult fecundity, but not for their interaction (Table 1). Fecundity decreased in both aphids in response to HA ($F_{2, 220} = 60.915$,

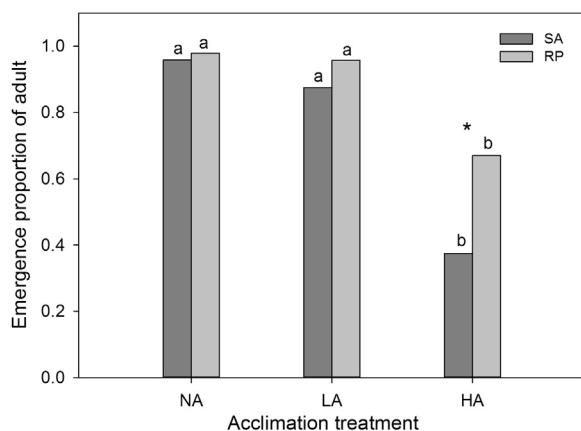


Fig. 3. Effects of developmental acclimation condition on the proportion of adult emergence. Different letters above the bars indicate significant differences between acclimation conditions for each species (Chi-square test, $P < 0.05$). “*” represents significant differences between the two species within each acclimation condition (Chi-square test, $P < 0.05$). SA = *Sitobion avenae*, RP = *Rhopalosiphum padi*.

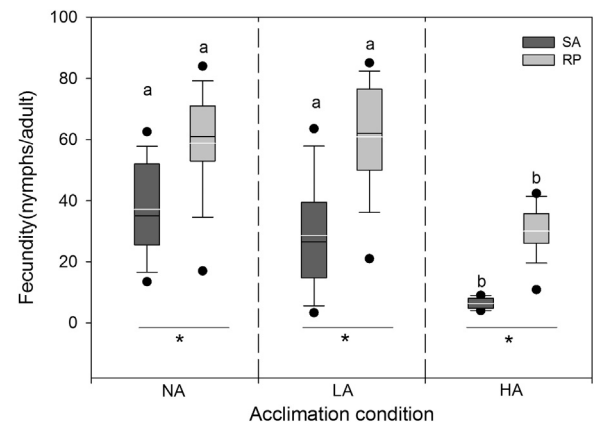


Fig. 4. Box plots of fecundity of *Sitobion avenae* (SA) and *Rhopalosiphum padi* (RP) after exposure to various developmental acclimation conditions. The white and black lines inside the boxes represent the mean and median values, respectively. Black dots mark the outliers (only showing 5th/95th). Different letters above the plots indicate significant differences between acclimation conditions for each species (one-way ANOVA, $P < 0.05$). “*” represents significant differences between the two species within each acclimation condition (t -test, $P < 0.05$).

$P < 0.001$). In comparison to a mean fecundity of 37.17 ± 15.54 nymphs per adult for *S. avenae* and 58.81 ± 17.51 nymphs per adult for *R. padi* in the NA treatment, fecundity substantially decreased (by 30.78 ± 2.44 and 28.84 ± 2.95 nymphs per adult, respectively) following exposure to HA. Additionally, the fecundity of *R. padi* was significantly higher than that of *S. avenae* under all acclimation conditions ($F_{1, 220} = 139.866$, $P < 0.001$) (Figs. 4 and 5).

3.3.2. Effect of developmental acclimation on adult longevity

There were significant effects of species, developmental acclimation condition and their interaction on adult longevity (Table 1). Longevity markedly decreased with increase in daily max-temperature, for both *S. avenae* ($F_{2, 103} = 15.135$, $P < 0.001$) and *R. padi* ($F_{2, 121} = 53.833$, $P < 0.001$). Compared to a mean longevity of 17.50 ± 7.58 d under NA, longevity was lower remarkably by 9.83 ± 1.18 d following HA exposure in *S. avenae*. While compared to a mean longevity of 24.66 ± 7.73 d under NA, longevity was remarkably lower

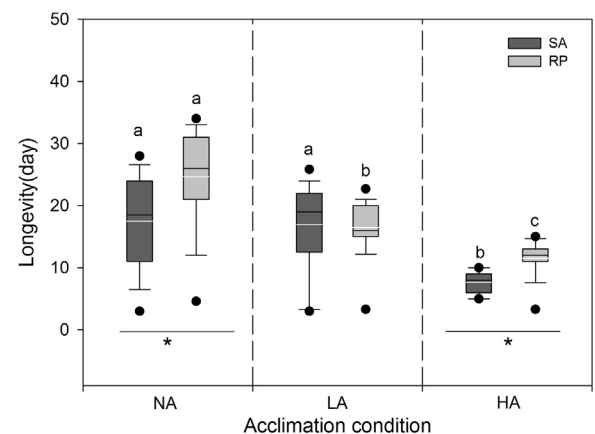


Fig. 5. Box plots of longevity of *Sitobion avenae* (SA) and *Rhopalosiphum padi* (RP) after exposure to various developmental acclimation conditions. The white and black lines inside the boxes represent the mean and median values, respectively. Black dots mark the outliers (only showing 5th/95th). Different letters above the plots indicate significant differences between acclimation conditions for each species (one-way ANOVA, $P < 0.05$). “*” represents significant differences between the two species within each acclimation condition (t -test, $P < 0.05$).

Table 2

Effects of developmental acclimation on population parameters in two aphid species. λ , finite rate of increase; r_m , intrinsic rate of population increase; R_0 , net reproductive rate; T , mean generation time. SA = *Sitobion avenae*, RP = *Rhopalosiphum padi*.

SA	λ	r_m	R_0	T	RP	λ	r_m	R_0	T
NA	1.2591	0.2304	32.5751	13.2884	NA	1.4373	0.3628	58.0322	9.3816
LA	1.2743	0.2424	25.3740	11.5056	LA	1.6120	0.4774	59.9959	7.2388
HA	1.1454	0.1357	3.6884	9.0947	HA	1.3606	0.3079	22.3615	8.8860

8.15 ± 1.32 and 13.13 ± 1.24 d following LA and HA, respectively, in *R. padi*. Moreover, longevity was higher for *R. padi* than for *S. avenae* (NA: $t = -4.507$, $df = 91$, $P < 0.001$; HA: $t = -5.230$, $df = 48$, $P < 0.001$), except in the case of LA ($t = 0.324$, $df = 69.834$, $P = 0.747$).

3.4. Effect of acclimation on population parameters

As is evident from the effects of developmental acclimation on the population parameters shown in Table 2, *R. padi* performed better than *S. avenae* in terms of population performance under all acclimation regimes. Conditions of high daytime temperature acclimation (38°C) led to an increase in detrimental effects on the intrinsic rate of population increase for both species (Fig. 6). In comparison to NA, LA induced an increase in r_m by 13% and 30% for *S. avenae* and *R. padi*, respectively, whereas HA decreased r_m by more than 80% for both species.

4. Discussion

4.1. Comparison of heat tolerance following acclimation in two aphid species

Our results indicate that *R. padi* has a higher basal tolerance than *S. avenae*. *Sitobion avenae* had previously been noted to possess lower thermal performance with respect to life history traits (Asin and Pons, 2001) and a higher capacity for behavioral thermal regulation (Ma and Ma, 2012). A long-term field investigation revealed that *R. padi* had replaced *S. avenae* as the dominant species in Yibin ($28^\circ46' \text{N}$) when high-temperature events became more frequent, from 1975 onwards (Huang et al., 1996). Given the expected increase in the frequency of heat events in the future (Easterling et al., 2000; Meehl and Tebaldi, 2004; Hansen et al., 2012), our evidence of thermal resistance in the two aphid species supports the prediction that *R. padi* will become predominant over *S. avenae* under climate warming scenarios (Ma et al., 2015).

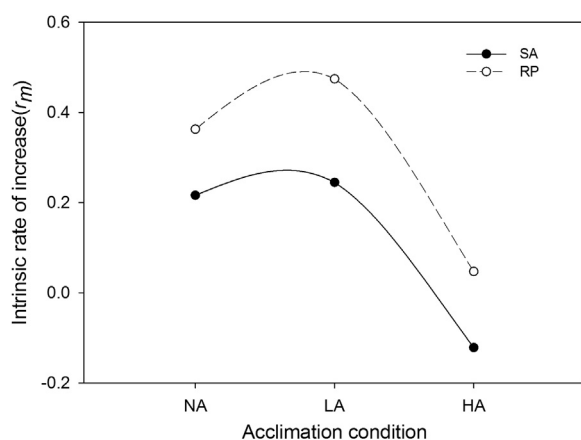


Fig. 6. Effects of developmental acclimation condition on the intrinsic rate of population increase in the two aphid species. SA = *Sitobion avenae*, RP = *Rhopalosiphum padi*.

In addition to differences in basal tolerance, our experiments also suggested species-specific changes in acclimation responses, where *R. padi* exhibited higher basal and inducible tolerances than did *S. avenae*. Both aphid species displayed an induced tolerance following LA (34°C), whereas substantial increases in plasticity beyond what was observed in response to LA was only observed in *R. padi*, when the daily maximum temperature was further increased to 38°C . In addition, a positive association between basal and inducible tolerance has been observed in our study, in agreement with investigations in geographic lines of *Drosophila buzzatii* (Loeschcke et al., 1994) and closely related species of *Deronectes* (Calosi et al., 2008). Overall, our results suggest that *R. padi* may have an advantage over *S. avenae* with respect to survival following exposure to heat events.

4.2. Fitness costs vary across developmental acclimation conditions in two aphid species

As expected, different levels of costs were observed in response to temperature acclimation in the two aphid species in the present study. In comparison to the 22°C constant temperature treatment, LA (34°C) had negligible impacts on survival (proportion of adult emergence) and reproductive (adult longevity and fecundity) traits of both species except for the longevity of *R. padi*, and even could improve population parameters. However, obvious costs related to survival, reproduction, and population parameters were detected in both species under HA (38°C), where *S. avenae* exhibited higher costs associated with these traits than *R. padi*. Our results suggest that the extent of fitness costs is influenced by the acclimation conditions and differs between species, which may offer a reasonable explanation for the contradictory reports that acclimation is both associated with fitness costs (Roux et al., 2010; Zhang et al., 2013) and that there is no cost to fitness (Hoffmann and Hewa-Kapuge, 2010). Species-specific costs may be related to the delayed death response (Xie et al., 2008; Mironidis and Savopoulou-Soultani, 2010), which is caused by heat injury and has been shown to be dependent on species tolerance (Denlinger and Yocum, 1998).

The magnitude of fitness costs were also influenced by acclimation conditions. In our experiments, temperatures were constant with the exception of the temperature-ramping phase of each acclimation treatment. Thus, the substantial cost under HA conditions (38°C) was likely to have been induced by the acute exposure to different temperatures during the temperature-ramping phase. The mean (31°C) and the maximum (38°C) temperatures of the temperature-ramping phase in the HA treatments were beyond the optimal temperatures for both *S. avenae* and *R. padi* [i.e., 26.5 and 28.5°C respectively; Asin and Pons (2001)]. In addition, while we observed that the adults of these aphid species can further increase their thermal tolerance in response to HA, this comes at substantial reproductive costs. The reproductive costs associated with exposure to higher acclimation temperatures could be linked to irreversible heat stress-related injuries, such as protein denaturation and alterations in both membranes and the structure of enzymes (Janssens and Stoks, 2017), water loss or dehydration (Piyaphongkul et al., 2014), and damage to the nervous system (Prosser and Nelson, 1981). In contrast, there could be several factors underlying the lack of fitness costs associated with low daytime developmental temperature acclimation (LA). First, the mean (28.8°C) and the maximum (34°C) temperatures of the temperature-ramping phase in LA

could induce hormesis to some extent, enabling the organisms to better resist stress and promote individual fitness (Minois, 2000; Scannapieco et al., 2007; Zhang et al., 2013). Secondly, metamorphic modularity (Campero et al., 2008; Potter et al., 2011) or compensatory growth (Stoks et al., 2006; Dmitriew and Rowe, 2007) can insulate against or counteract the damage arising from low daytime temperature acclimation during early life history stages.

5. Conclusion

Our results indicate that fitness costs vary in response to developmental acclimation temperatures and in a species-specific manner in the aphid species investigated in the present study (i.e., *S. avenae* and *R. padi*). This conclusion offers a framework for understanding the population dynamics of pest species in the face of increases in global temperatures, and could also potentially improve pest control efforts. For example, the thermal resistance of insects introduced as a biological control agent for targeted pest control could be improved by exposing them to acclimation temperatures without incurring fitness costs prior to release (Hoffmann and Hewa-Kapuge, 2010).

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